

Canis lupus. By L. David Mech

Published 2 May 1974 by The American Society of Mammalogists

Canis lupus Linnaeus, 1758 Gray Wolf

- Canis lupus* Linnaeus, 1758:39. Type locality Sweden.
Canis lycaon Schreber, 1775:pl. 89. Type locality Quebec, Quebec, by restriction (Goldman, 1937:38).
Canis Lupus-Griseus Sabine, in Franklin, 1823:654, not *Griseus* Boddaert, 1794.
Canis Lupus-Albus Sabine, in Franklin, 1823:655, not *albus* Kerr, 1792.
Canis nubilus Say, in Long, 1823:169. Type locality Engineer Cantonment, approximately 2 mi. N Ft. Calhoun, Washington County, Nebraska.
Canis pallipes Sykes, 1831:101. Type locality Deccan, India.
Canis hodophilax Temminck, 1839:284. Type locality Hondo, Japan.
Canis variabilis Wied-Neuwied, 1841:95. Type locality Fort Clark, near Stanton, Mercer County, North Dakota.
Lupus orientalis Wagner, 1841:367. Type locality Europe.
Lupus laniger Hodgson, 1847:474. Type locality "Tibet," but possibly little Tibet in Kashmir.
Canis chanco Gray, 1863:94. Type locality Chinese Tartary.
Canis niger Selater, 1874:pl. 78, not *niger* Kerr, 1792.
Canis pambasileus Elliot, 1905:79. Type locality Susitna River, region of Mt. McKinley, Alaska.
Lupus filchneri Matschie, 1908:153. Type locality Siningfu, Kansu, China.
Lupus karanorensis Matschie, 1908:159. Type locality Karanor, in the Gobi.
Lupus tschiliensis Matschie, 1908:160. Type locality Coast of Chihli, China.
Lupus altaicus Noak, (?) 1911:465. Type locality Chulyshman Glacier, Altai.
Canis tundrae Miller, 1912:1. Type locality Point Barrow, Alaska.

CONTEXT AND CONTENT. Order Carnivora, Family Canidae. The genus *Canis* includes eight species. Approximately 24 New World and eight Old World subspecies of *C. lupus* are recognized, the number depending on authorities accepted. For summary, see Mech (1970); for full synonymy, see Pocock (1935), Goldman (1944), Ellerman and Morrison-Scott (1951), Novikov (1956), and Hall and Kelson (1959).

- C. l. lupus* Linnaeus, 1758:39, see above (synonyms are *flavus* Kerr, *niger* Hermann, *communis* Dwigubski, *orientalis* Wagner, *major* Ogérien, *minor* Ogérien, *deitanus* Cabrera, *signatus* Cabrera, *lycaon* Trouessart, *altaicus* Noak, *italicus* Altobello, and *kurjak* Bolka).
C. l. lycaon Schreber, 1775:pl. 89, see above (synonyms are *canadensis* Blainville and *ungavensis* Comeau).
C. l. albus Kerr, 1792:137. Type locality Jenisea eastern USSR (synonyms are *turuchanensis* Ognev, and *dybowskii* Domaniewski).
C. l. campestris Dwigubski, 1804:10. Type locality between Black Sea and Caspian, Kirghizia, to Yenesei River (synonyms are *desertorum* Bogdanov, *cubanensis* Ognev).
C. l. nubilus Say, 1823:169, see above (a synonym is *variabilis* Wied-Neuwied).
C. l. occidentalis Richardson, 1829:60. Type locality Simpson, Mackenzie, Canada (synonyms are *sticta* Richardson, *ater* Richardson).
C. l. pallipes Sykes, 1831:101, see above.
C. l. hodophilax Temminck, 1839:284, see above (synonyms are *hodopylax* (sic) Temminck and *japonicus* Nehring).
C. l. juscus Richardson, in Beechey, 1839:5. Type locality Columbia River below the Dalles, between Oregon and Washington, USA (a synonym is *gigas* Townsend).
C. l. chanco Gray, 1863:94, see above (synonyms are *laniger* Hodgson, *niger* Selater, *filchneri* Matschie, *karanorensis* Matschie, *tschiliensis* Matschie, and *coreanus* Abe).
C. l. griseoalbus Baird, 1858:104. Type locality Cumberland

- House, Saskatchewan, Canada (synonyms are *Lupus-Griseus* Sabine, and *knightii* Anderson).
C. l. pambasileus Elliot, 1905:79, see above.
C. l. tundrae Miller, 1912:1, see above.
C. l. baileyi Nelson and Goldman, 1929:165. Type locality Colonia Garcia, Chihuahua, Mexico.
C. l. hattai Kishida, 1931:73. Type locality Sapporo, Hokkaido, Japan (*rex* Pocock is a synonym).
C. l. crassodon Hall, 1932:420. Type locality Tahsis Canal, Nootka Sound, Vancouver Island, B.C., Canada.
C. l. arabs Pocock, 1934:636. Type locality "Ain in S.E. Arabia."
C. l. orion Pocock, 1935:683. Type locality "Cape York, on Baffin Bay, N.W. Greenland."
C. l. arctos Pocock, 1935:682. Type locality "Melville Island, Arctic America."
C. l. beothucus G. M. Allen and Barbour, 1937:230. Type locality "Newfoundland, Canada."
C. l. irremotus Goldman, 1937:41. Type locality "Red Lodge, Carbon County, southwestern Montana," USA.
C. l. labradorius Goldman, 1937:38. Type locality "vicinity of Fort Chimo, Quebec, Canada."
C. l. ligoni Goldman, 1937:39. Type locality "head of Duncan Canal, Kupreanof Island, Alexander Archipelago, Alaska," USA.
C. l. mogollonensis Goldman, 1937:43. Type locality "S.A. Creek, 10 miles northwest of Luna, Catron County, New Mexico," USA.
C. l. monstabilis Goldman, 1937:42. Type locality "10 miles south of Rankin, Upton County, Texas," USA.
C. l. youngi Goldman, 1937:40. Type locality "Harts Draw, north slope of Blue Mountains, 20 miles northwest of Monticello, San Juan County, Utah," USA.
C. l. alces Goldman, 1941:109. Type locality Kachemak Bay, Kenai Peninsula, Alaska, USA.
C. l. columbianus Goldman, 1941:110. Type locality Wistaria, N. side Ootsa Lake, B.C., Canada.
C. l. hudsonicus Goldman, 1941:112. Type locality head of Schultz Lake, Keewatin, Canada.
C. l. bernardi Anderson, 1943:389. Type locality Cape Kellett, SW Banks Island, Franklin, Canada.
C. l. mackenzii Anderson, 1943:388. Type locality Imnanuit, west of Kater Point, Bathurst Inlet, Mackenzie, Canada (a synonym is *Lupus-Albus* Sabine).
C. l. manningi Anderson, 1943:392. Type locality Hantzch River, east Foxe Basin, west side Baffin Island, Franklin Canada.

DIAGNOSIS AND GENERAL CHARACTERS. Largest member (figure 1) of the Canidae except for certain breeds of domestic dogs (*Canis familiaris*). Adult females weigh from 18 to 55 kg (40 to 120 lb) and measure 1.37 to 1.52 m (4.5 to 6.0 ft) in total length; and males 20 to 80 kg (45 to 175 lb) and 1.27 to 1.64 m (5.0 to 6.5 ft), depending on subspecies. Fur long and varying in color from pure white through mottled gray and brown to coal black; usually grizzled gray. Generally resembling domestic German shepherd or husky in head and body configuration but distinguishable from them by having orbital angle (figure 2) of 40° to 45° as compared with 53° to 60° in dogs (Iljin, 1941) and having large, convex, and almost spherical tympanic bullae as compared with smaller, compressed, and slightly crumpled bullae in dogs. Distinguishable from coyote (*Canis latrans*) by having larger size, broader snout, relatively shorter ears, and proportionately smaller brain case. *Canis rufus* of eastern Texas and Louisiana is similar to *Canis lupus*, being intermediate in many characters between wolf and coyote (Nowak, 1970). See "Remarks." Further distinctions among these four closely related and similar animals were detailed by Lawrence and Bossert (1967).

DISTRIBUTION. Formerly throughout Northern Hemisphere north of 20° N latitude (figure 3) in all habitats and topography except deserts and high mountain tops. Deliberate



FIGURE 1. Adult *Canis lupus*, photo by the author.

extermination has restricted present range in North America (see figure 4), and in the Old World to eastern Europe, the Soviet Union, China, and northern India. Remnant populations live in western Europe and Scandinavia.

FOSSIL RECORD. A closely related Pleistocene species was found in Cumberland Cave, Maryland (Gidley, 1913).

FORM. Guard hairs are 60 to 100 mm long (120 to 150 mm in mane) with imbricate scales that are elongate in proximal region of hair, crenate medially, and flattened distally; underfur has coronal scales (Adorjan and Kolenosky, 1969). Dorsal hairs are generally longer and darker than those of venter; a group of stiff hairs surrounds the precaudal gland on dorsal side of tail about 70 mm from base. Hildebrand

(1952) has described details of the integument in the Canidae. Shedding occurs in late spring.

The front foot has five toes, including a short one with a dew claw proximad from other four; the hind foot has four toes. Limb posture is digitigrade; the chest is narrow and keel-like with forelimbs seemingly pressed into chest, and elbows turned inward and paws outward (Young, 1944; Iljin, 1941). The legs are moderately long. Dentition i 3/3, c 1/1, p 4/4, m 2/3, total 42; canines are about 26 mm long and carnassials are well developed. The cranium is elongate and tapering anteriorly, with long jaws (figure 5). For further details on skull and teeth see Goldman (1944). The baculum is pointed and has a ventral groove. The especially strong and large masseter muscles allow a powerful bite.

Atkins and Dillon (1971) have compared the brain to that of other canids.

The simple stomach can hold 7 to 9 kg (15 to 20 lb) of food. The liver is relatively large, varying in males from 0.7 to 1.9 kg (1.6 to 4.2 lb) and averaging 1.2 kg (2.6 lb) and in females .68 to .82 kg (1.5 to 1.8 lb) (Makridin, 1962). Except for minor differences noted in "Diagnosis," anatomy is similar to that of the domestic dog. There normally are 10 mammae (Goldman, 1944).

FUNCTION. Fine underfur and long guard hairs conserve a high proportion of body heat, enabling wolves to function in temperatures lower than -40° F. Tireless travel at a usual rate of 8 km per hour and a running gait of 55 to 70 km per hour is facilitated by the animal's long legs and powerful leg muscles (Mech, 1970). The extended rostrum provides abundant surface for the olfactory organ, allowing the wolf to detect odors of prey at distances up to 2.4 km (1.5 mi) under favorable conditions (Mech, 1966). Digestion of food may take place within a few hours (Makridin, 1959). Howling and scent marking via urine posts, feces, and scratching are common and may function in territory maintenance, although direct evidence for this hypothesis is lacking. Growling, with a frequency of 380 to 450 Hz, and barking, at 320 to 904 Hz (Tembrock, 1963), are both at times manifestations of threat. The howling of three adult males was described as follows: "[The howl is] a continuous sound from half a second to 11 seconds in length. It consists of a fundamental frequency which may lie between 150 and 780 cycles per second [Hz], and up to 12 harmonically related overtones. Most of the time, the pitch remains constant

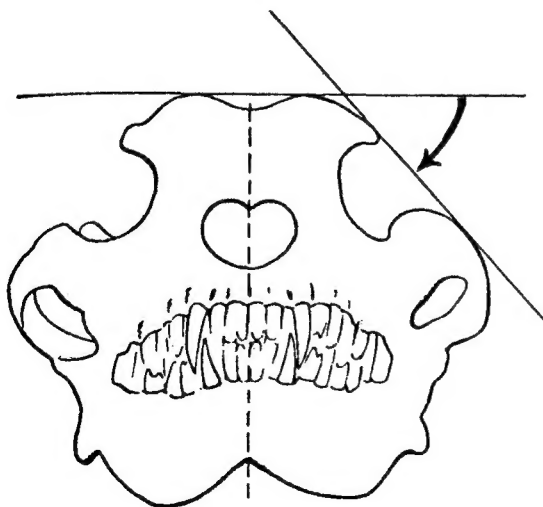


FIGURE 2. Anterior view of wolf skull to show the orbital angle, which is 40° to 45° as opposed to more than 53° in dogs (from Iljin, 1941).

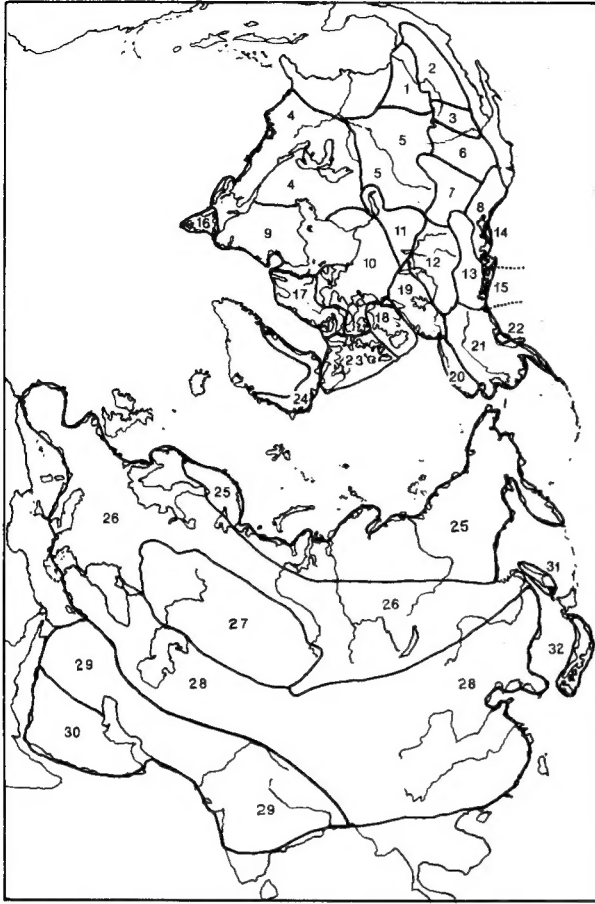


FIGURE 3. North circumpolar projection of Holarctic Region to show the original range of *Canis lupus* and the following subspecies: 1. *C. l. monstrabilis*, 2. *C. l. baileyi*, 3. *C. l. mogollonensis*, 4. *C. l. lycaon*, 5. *C. l. nubilus*, 6. *C. l. youngi*, 7. *C. l. irremotus*, 8. *C. l. fuscus*, 9. *C. l. labradorius*, 10. *C. l. hudsonicus*, 11. *C. l. griseoalbus*, 12. *C. l. occidentalis*, 13. *C. l. columbianus*, 14. *C. l. crassodon*, 15. *C. l. ligoni*, 16. *C. l. beothucus*, 17. *C. l. manningi*, 18. *C. l. bernardi*, 19. *C. l. mackenzii*, 20. *C. l. tundrarum*, 21. *C. l. pambasileus*, 22. *C. l. alces*, 23. *C. l. arctos*, 24. *C. l. orion*, 25. *C. l. albus*, 26. *C. l. lupus*, 27. *C. l. campestris*, 28. *C. l. chanco*, 29. *C. l. pallipes*, 30. *C. l. arabs*, 31. *C. l. hattai*, and 32. *C. l. hadrophilax*.

or varies smoothly, and may change direction as many as four or five times. Total intensity does not greatly vary throughout" (Theberge and Falls, 1967). Howling by one pack of wolves may stimulate howling in adjacent packs.

REPRODUCTION AND ONTOGENY. After courtship that may last from days to months, wolves copulate during an estrus of 5 to 7 days. Blood may flow from the vulva for a few days to a few weeks before estrus. The receptive period may be anytime from January in low latitudes to April in high latitudes. Many courtship attempts are made, but few succeed (Rabb *et al.*, 1967). Courtship may take place between adult members of packs or between lone wolves that pair during the mating season. Copulation involves typical canid coupling in which the bulbous base of the penis locks into the vaginal sphincter, and the tie may last for more than 30 minutes. In dogs, and presumably wolves, ejaculation occurs intermittently during the tie. Definite mate preferences are shown, but not all courtship or copulation by members of a pair is directed at the mate. Maturing females may come into heat 2 weeks later than animals that have bred before (Rausch, 1967). In Alaska, mature females shed an average of 7.3 ova and implant 6.5 embryos, and newly maturing females, 6.1 ova and 5.4 embryos (Rausch, 1967). Gestation lasts 63 days, and an average of six young (extremes, one to 11) are born blind and helpless, usually in a hole in the ground, but often in a rock crevice, hollow log, overturned stump, or other place of quiet and shelter. The same den is sometimes used year after year. The female usually stays near the young for at least 2 months,

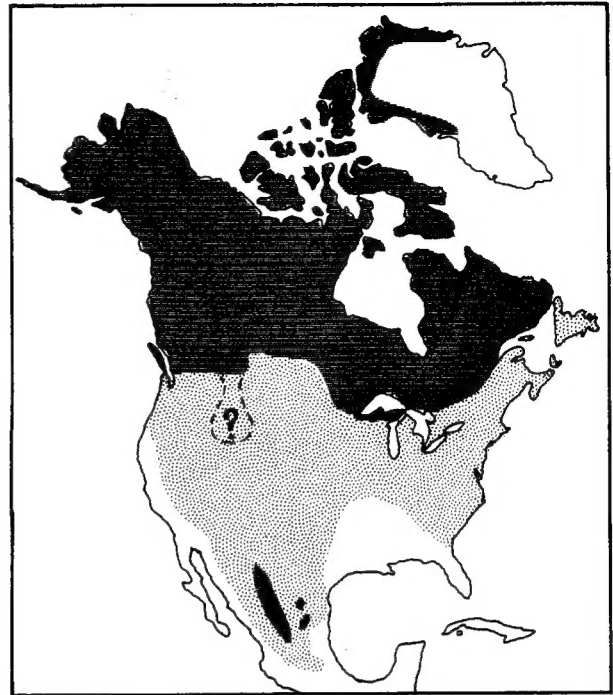


FIGURE 4. Range of the gray wolf in North America prior to settlement by Europeans and reduced range today (darker shading in the north and in Mexico). An area in western Montana and adjacent parts of Idaho and Wyoming where populations are perhaps becoming reestablished is shown with a question mark.

while the male and other pack members hunt and feed both the female and the pups. Eyes open at day 11 to 15, most milk teeth are present by about week 3, and weaning takes place at about week 5. After about week 8, the pups are moved to a ground nest, where they romp and play over an area of up to an acre (.4 hectare) an area known as a "rendezvous site." The pups may spend up to 3 weeks at one site but are then shifted as far away as 8 km (5 mi) to another. Probably depending on the degree of development of pups, they may continue this behavior even through winter, although pups in good physical condition will join adult members of a pack in their travels as early as October, at which time they may weigh 27 kg (60 lb) and be almost of adult size. Adult teeth replace deciduous teeth between weeks 16 and 26 (Schonberger, 1965). Epiphyseal cartilage calcifies about month 12 (Rausch, 1967). Wolves may gain sexual maturity in year 2 but often do not breed until 3. In populations unexploited by man, only about 60% of the adult females breed (Pimlott *et al.*, 1969), whereas in exploited populations 90% may breed (Rausch, 1967). Wolves may live 16 years (Young, 1944), but 10 years is an old age for individuals in the wild.

ECOLOGY. Wolves originally occupied most habitats in the Northern Hemisphere. They are predators on large mammals primarily, including deer (*Odocoileus*), moose or Old World elk (*Alces alces*), red deer or wapiti or New World elk (*Cervus elaphus*), caribou (*Rangifer tarandus*), bison (*Bison bison*), musk-oxen (*Ovibus moschatus*), mountain sheep (*Ovis*), and mountain goats (*Oreamnos americanus*). Beaver (*Castor canadensis*) is the smallest consistent prey reported, although almost any species of animal may be eaten, including any type of domestic animal. Most analyses of wolf predation on wild species have shown that young, old, and otherwise inferior members of prey populations constitute most of the animals killed by wolves (summarized by Mech, 1970; see also Mech and Frenzel, 1971). Less than 8% of attacks by a pack of 15 wolves on moose were successful on Isle Royale, Michigan, where the major prey is moose (Mech, 1966). Chases ranging from 100 m to 5 km are the rule. Wolves first attack the rump of larger prey, but the head, shoulders, flanks, or rump of deer. Hamstringing has not been documented with wild prey. Usually all of the prey is eaten except for the larger bones and chunks of hide. Average kill rates vary from one deer per wolf per 18 days (Mech and Frenzel, 1971) to one

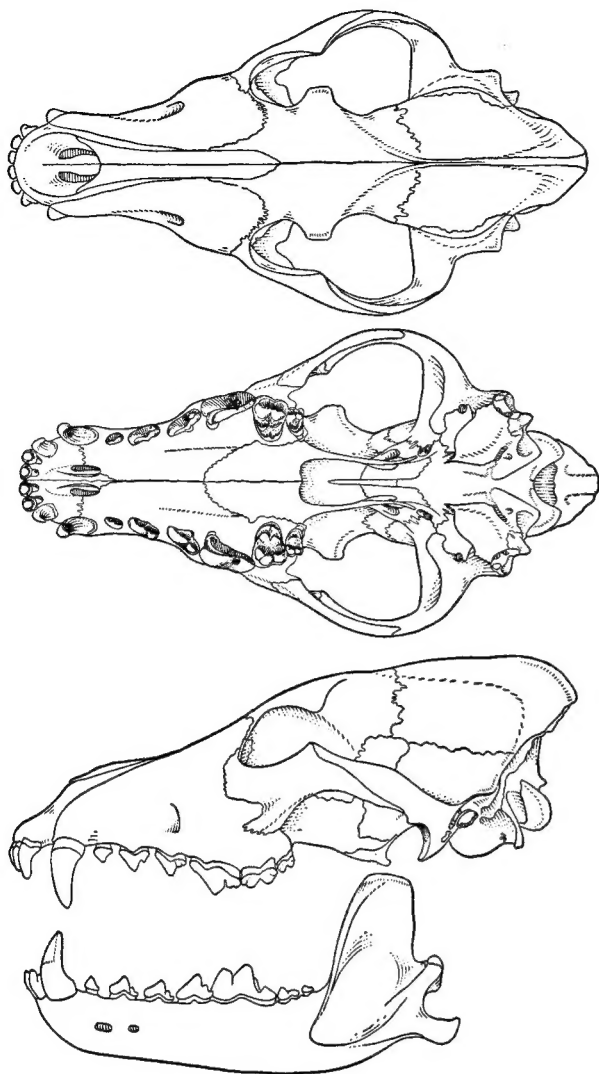


FIGURE 5. Skull of *Canis lupus tundrarum* from Wahoo Lake, Alaska (after Bee and Hall, 1956:169).

moose per wolf per 45 days (Mech, 1966), with corresponding average estimated consumption rates being 2.5 kg (5.6 lb) of deer per wolf per day to 6.3 kg (13.9 lb) of moose per wolf per day. Remains of kills often supply food to such scavengers as ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), foxes (*Vulpes*), and other small birds and mammals. Ravens frequently follow wolf packs for miles, evidently in search of such food.

According to Mech (1970) who summarized the reports of parasites in wolves, the following have been recorded: nine species of flukes (Trematoda), 21 species of tapeworms (Cestoda), 24 species of roundworms (Nematoda), three species of spiny-headed worms (Acanthocephala), two species of lice, one species of flea, seven species of ticks, one species of tongue worm, and one species of mange mite. Probably the most important parasite of the wolf is *Echinococcus granulosus*, the hydatid tapeworm, the larval stage of which can infect man. Diseases known for the wolf include rabies, distemper, arthritis, cancer, and miscellaneous other disorders (Mech, 1970).

Few animals compete successfully with the wolf, except for man and perhaps the cougar (*Felis concolor*). There is some evidence (Mech, 1970) that high densities of wolves may reduce populations of the coyote (*Canis latrans*), wolverine (*Gulo gulo*), and lynx (*Lynx canadensis*).

The age structure of wolves in an unexploited population in Ontario was 35% pups, 40% yearlings, and 25% adults (Pimlott *et al.*, 1969), whereas in an exploited population in Alaska it was 42% pups, 29% yearlings, and 30% adults (Rausch, 1967). Mech (1970) has calculated that survival

rates of wolves in unexploited populations are 6 to 43% for pups from birth to first winter, 55% from first to second winter, and about 80% annually for adults. Mortality factors include diseases, parasites, starvation, intra-specific strife, injuries by prey, and exploitation and persecution by human beings.

Wolves travel a great deal, usually more at night but often during the day if the temperature is cool (Mech, 1970). Three types of movements can be distinguished—(1) travels within home range, (2) dispersal, and (3) migrations. Home range sizes vary from 130 km² (50 mi²) in Minnesota (Mech and Frenzel, 1971) to 13,000 km² (5000 mi²) in Alaska (Burkholder, 1959). Daily travels within home range vary from a few kilometers per day to up to 72 (45 miles). A dispersing wolf traveled a straight-line distance of 206 km (129 mi) in 2 months (Mech and Frenzel, 1971). In tundra areas, wolves follow migrating caribou herds and thus annually travel more than 160 km (100 mi), one way, from tundra to taiga and back (Kelsall, 1968). The farthest that individual migrating wolves have been known to travel is 360 km (225 mi) (Kuyt, 1972). Studies in progress in Minnesota (Mech, unpublished) show that family groups or packs occupy exclusive home ranges, and that lone wolves cover much larger areas, shifting about amongst these, and being chased by the resident packs. Highest known natural density of wolf populations anywhere on a year-around basis is one wolf per 26 km² (10 mi²) on the average (Pimlott, 1967).

Few other species have had such a diversity of relationships with man as has the wolf. Evidently early humans tamed wolves and domesticated them, eventually selectively breeding them and finally developing the domestic dog (*Canis familiaris*) from them. At present, the taming of wolves for pets continues, a process not difficult if considerable time is devoted to it, and wolf farms now sell pups for \$100 to \$325 each. Most of these animals end up in zoos. Because of the wolf's habit of killing domestic livestock, the species was exterminated by bounties, poisoning, and government control programs in more than 95% of the area of the 48 contiguous United States, in much of Mexico, in the settled farming areas of Canada, in most of western Europe, and in much of eastern Europe and the Soviet Union. In the latter two areas, concerted programs of extermination continue (Pullianen, 1965), although there is some evidence that official policy toward the wolf in the USSR is changing (Oshanin, 1971). Various Canadian provinces still pay bounties on wolves, although in most of these areas little damage to livestock is done. The wolf is informally considered in danger of extinction in Mexico. In the United States outside of Alaska, six of the eight subspecies that originally occurred at least in part in the country are now considered extinct there, (*C. l. lycaon* and *C. l. irremotus* are officially on the Secretary of the Interior's list of endangered animals). The possibility of the occurrence of some *C. l. nubilus* in Minnesota has been raised by Mech and Frenzel (1971). In Alaska, there are restrictions on taking wolves in some areas, and bounties on them in others (Harper, 1970). Wolves are legally protected in Michigan, where a small remnant population exists, in Wisconsin, where there may be a few individuals, and in Isle Royale National Park, where the population numbers 20 to 30 (Mech, 1966; Jordan *et al.*, 1967). In the Superior National Forest of Minnesota, wolves are protected by federal law, although state laws allow almost unrestricted taking, and in some parts of Minnesota state control programs offering \$50 per animal killed are in effect. Several hundred wolves are still present in the state, with an estimated 300 to 400 living in Superior National Forest (Mech, 1973).

Wolf fur is used for parkas, mukluks, and rugs. Raw wolf pelts from forested areas sell for \$15 to \$100 depending on quality and color. Arctic wolves bring higher prices than those from other regions. Wolves are hunted for sport in parts of Alaska and Canada, usually with an aircraft searching for the animals on frozen lakes or open tundra. Trapping wolves for fur and bounty remains lucrative for some Indians, Eskimos, and a few whites.

The main methods of studying wolves have been natural observation in open areas, aerial tracking and observation in winter, live-trapping via steel traps and snares with locks, and tagging with radio-collars. For anesthetizing wild-caught wolves, a combined intramuscular injection of 30 mg of phencyclidine hydrochloride and 25 mg of promazine hydrochloride has been successful (Seal and Erickson, 1969; Mech and Frenzel, 1971). Censusing has proved difficult because of low density and extensive areas involved. In limited areas, extensive aerial observations in winter have allowed reasonably accurate estimates (Mech, 1966, 1973; Pimlott *et al.*, 1969).

BEHAVIOR. The wolf is a social animal, usually functioning in packs that are basically family groups (Mech, 1970). Packs usually contain 5 to 8 members, but packs of up to 36 have been reported (Rausch, 1967). Packs are held together by strong affectional ties that develop, are reinforced, and become fixed in pups during the first 5 months of life, or by courtship behavior between two lone mature adults. Order is maintained in the pack by a dominance hierarchy with the adult male dominant to the adult female and pups, the female dominant to the pups, and a linear order among the pups. In larger packs a male order and female order develops among adults, but the leader is almost always a male, known as the "alpha male."

In most interactions between two wolves, one greets the other by demonstrating its dominance, while the other indicates submission (Schenkel, 1947). The dominant posture includes a stiff-legged stance, ears erect and forward, lips pulled forward, mane bristling, and tail vertical. The teeth may be bared, and there may be growling. There are two types of submission, active and passive. Active submission is less intense and involves drawing back of the lips and ears, rapid thrusting out of the tongue, lowering of the hind quarters, and pulling of the tail alongside or between the legs. The entire body is usually lowered and the muzzle is pointed up toward the mouth of the dominant animal and may touch it. This is often accompanied by whining and urinating. In passive submission, which is more intense, the wolf rolls onto its back and draws in its paws toward its body, and often urinates. According to Schenkel (1967), this behavior develops from the elimination posture of young pups in which the adult licks the perineal area, stimulating and ingesting the waste of the pup. Active submission develops from a food-begging posture in pups, which causes the adults to regurgitate food to them, the usual method of weaning and feeding of pups for the first several months of their life. Social rank in pups is probably established normally through play-fighting, but two pups raised by Mech (1970), apart from their parents, fought seriously at the age of 30 days, established their relative ranks at that time, and never fought after that. Social interactions and dominance demonstrations occur every day throughout the year but intensify during the breeding season. At that time some shifts in rank may take place, but these only occur among adult members. Only rarely is intrapack fighting resorted to.

Courtship between previously unmated wolves may take place several months before breeding (Crisler, 1958) or just a few days before the breeding season (Mech, unpublished). Courtship consists of a great deal of sniffing, nipping, head rubbing, snout grabbing, tail wagging, and general play with considerable body contact. Either male or female may place a paw or neck across the back of the other. The female, when receptive, will lift her tail and display her vulva. Mounting may take place from the side initially but is soon oriented from behind, with the male grasping the female around the chest and inserting his penis, and thrusting until the bulbous base of his penis is locked behind the vaginal sphincter. While the pair is still locked together by their genitals the male dismounts, lifts a hind leg over his partner's back and turns his body 180° away from her. The pair then remain coupled, back to back, for as long as 30 minutes, during which ejaculation occurs many times.

There are three main methods of communication among wolves: (1) howling and other vocalizations; (2) visual displays including postures and positions of various body parts, especially the face; and (3) scent-marking. It is known that individual wolves may have distinctive howls (Theberge and Falls, 1967). The howling of pups is usually high-pitched, with considerable yapping, whereas the pitch of adults is much lower. One of the functions of howling is in assembling the pack, and territory advertisement is suspected as another. Coarse barking, whining, and growling are other vocalizations. Body positions and facial expressions show social status primarily, as described above. Inguinal presentation and sniffing are also involved in status demonstrations, but probably also serve in individual identification. Scent-marking (Kleiman, 1966) involves deposition of urine and/or feces on conspicuous objects along trails, and often includes intense scratching of the earth. It is usually performed by high-ranking adult males, often at trail intersections (Mech and Frenzel, 1971). It is speculated that scent-marking is a means of advertising territory, but this has not been proved.

Wolves are good swimmers and do not hesitate to wade or swim across rivers and lakes; they sometimes follow prey into water even in winter (Pimlott *et al.*, 1969). Wolves rest on their sides usually, although they sometimes rest on their

abdomen; when sleeping deeply, they lie curled up with nose beneath tail. Play involves chasing, ambushing, and mock fighting, and these activities may help each pup determine its social status among its peers. Behavior of wolves has been studied with captive packs (Schenkel, 1947; Rabb *et al.*, 1967), by long-range observation (Murie, 1944), and through the use of aircraft in winter (Mech, 1966; Jordan *et al.*, 1967; Haber, 1973). Extensive studies comparing the behavior of wolves in captivity with that of other canids are being conducted by Fox (1972).

GENETICS. To date no differences in karyotypes have been found between the wolf and the domestic dog or the coyote (Hungerford and Snyder, 1966), or the red wolf (Nowak, 1970). According to Hsu and Benirschke (1967), both dog and coyote have 39 pairs of chromosomes, with the autosomes described as "acrocentrics or teleocentrics" and the sex chromosomes as "submetacentric" for the X and "minute" for the Y in the coyote and "minute metacentric" for the Y in the dog. Iljin (1941) crossed a wolf with a black mongrel sheep dog and then made various types of crosses for four generations, totaling 101 individuals, all of which were fertile.

REMARKS. Jolicœur (1959) concluded that there are probably far too many subspecies of *Canis lupus* recognized, and the author concurs. Some of the subspecies have been described on the basis of only a few specimens.

The relationship between *Canis lupus* and the red wolf (*C. rufus*) is unclear, but Lawrence and Bossert (1967) presented evidence that *C. rufus* may be a subspecies of *lupus* or may be a hybrid between *lupus* and *latrans*. Paradiso (1968), Nowak (1970), and Atkins and Dillon (1971) treat *rufus* as a distinct species.

Goldman (1944) summarized the taxonomy of the wolves of North America, and Young (1944) presented considerable historical information about the species. Rutter and Pimlott (1968) condensed much of the ecological and behavioral material on the wolf for popular consumption, and Mech (1970) synthesized most of the technical information that was available about the animal through 1968. Fox (1972) detailed the behavior of wolves in comparison with other canids.

Financial support for preparation of this account came from the Welder Wildlife Fund and the World Wildlife Fund.

LITERATURE CITED

- Adorjan, A. S., and G. B. Kolenosky. 1969. A manual for the identification of hairs of selected Ontario mammals. Ontario Dept. Lands and Forests Res. Rept. (Wildlife) 90:1-64.
- Allen, G. M., and T. Barbour. 1937. The Newfoundland wolf. Jour. Mammal. 18:229-234.
- Anderson, R. M. 1943. Summary of the large wolves of Canada, with descriptions of three new Arctic races. Jour. Mammal. 24:386-393.
- Atkins, D. L., and L. S. Dillon. 1971. Evolution of the cerebellum in the genus *Canis*. Jour. Mammal. 52:96-107.
- Baird, S. F. 1858. Mammals. In Reports of Explorations and Surveys . . . Washington, D.C., vol. 8, pt. 1, 764 pp.
- Bee, J. W., and E. R. Hall. 1956. Mammals of Northern Alaska. . . Misc. Publ. Mus. Nat. Hist., Univ. Kansas 8:1-309.
- Beechey, F. W. 1839. The zoology of Capt. Beechey's voyage . . . 1825-28. Mammalia by J. Richardson. London, 180 pp.
- Burkholder, B. L. 1959. Movements and behavior of a wolf pack in Alaska. Jour. Wildlife Mgt. 23:1-11.
- Crisler, Lois. 1958. Arctic wild. Harper and Bros., N.Y. 301 pp.
- Ellerman, J. R., and T. C. S. Morrison-Scott. 1951. Checklist of Palaearctic and Indian mammals. . . British Museum (Nat. Hist.), London, 810 pp.
- Elliot, D. G. 1905. A checklist of mammals of the North American continent, the West Indies, and the neighboring seas. Field Columbian Mus., Publ. 105, Zool. Ser. 6:1-761.
- Fox, M. W. 1972. The behavior of wolves, dogs, and related canids. Harper and Row, New York, 220 pp.
- Franklin, John. 1823. Narrative of a journey to the shores of the polar sea. . . John Murray, London, 768 pp. + 30 pls., 4 maps.
- Gidley, J. W. 1913. Preliminary report on a recently discovered Pleistocene cave-deposit near Cumberland, Maryland. Proc. U.S. Nat. Mus. 46:93-102.
- Goldman, E. A. 1937. The wolves of North America. Jour. Mammal. 18:37-45.

- 1941. Three new wolves from North America. *Proc. Biol. Soc. Washington* 54:109-114.
- 1944. The wolves of North America. Classification of wolves. *The Amer. Wildl. Inst. Washington, D.C.*, part 2, pp. 387-636.
- Gray, J. E. 1863. Notice of the chanco or golden wolf (*Canis chanco*) from Chinese Tartary. *Proc. Zool. Soc. London*, p. 94.
- Haber, G. C. 1973. Eight years of wolf research at McKinley Park, Alaska, pp. 7-9, 52-57 (April), pp. 43-45, 50, 53-56 (May).
- Hall, E. R. 1932. Remarks on the affinities of the mammalian fauna of Vancouver Island, British Columbia, with descriptions of new subspecies. *Univ. California Publ. Zool.* 38:415-423.
- Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. The Ronald Press, New York 2:viii + 547-1083.
- Harper, J. 1970. Wolf management in Alaska. Pp. 24-27, in (S. E. Jorgensen, C. E. Faulkner, and L. D. Mech, eds.) *Proceedings of a Symposium on Wolf Management in North America* U. S. Bureau of Sport Fisheries and Wildlife, Minneapolis, 50 pp.
- Hildebrand, M. 1952. The integument in Canidae. *Jour. Mammal.* 33:419-428.
- Hodgson, B. H. 1847. Description of the wild ass (*Asinus polydon*) and wolf of Tibet (*Lupus laniger*). *Calcutta, Jour. Nat. Hist.* 7:474.
- Hsu, T. C., and K. Benirschke. 1967. An atlas of mammalian chromosomes. 1:folios 20, 21.
- Hungerford, D. A., and R. L. Snyder. 1966. Chromosomes of a European wolf (*Canis lupus*) and of a bactrian camel (*Camelus bactrianus*). *Mammal. Chromosome Newsl.* 20: 72.
- Iljin, N. A. 1941. Wolf-dog genetics. *Jour. Genetics* 42: 359-414.
- Jolicoeur, P. 1959. Multivariate geographical variation in the wolf *Canis lupus* L. *Evolution* 13:283-299.
- Jordan, P. A., P. C. Shelton, and D. L. Allen. 1967. Numbers, turnovers, and social structure of the Isle Royale wolf population. *Amer. Zool.* 7:233-252.
- Kelsall, J. P. 1968. The caribou. *Canadian Wildlife Serv. Monogr.* 3:1-340.
- Kishida, K. 1931. [Title unknown; paper issued as preprint from number of journal that was never printed]. *Lansahia* 3(25):72-75.
- Kleiman, Devra. 1966. Scent marking in the Canidae. *Symp. Zool. Soc. London* 18:167-177.
- Kuyt, E. 1972. Food habits of wolves on barren-ground caribou range. *Canadian Wildlife Serv., Rept. Ser.* 21: 1-36.
- Lawrence, Barbara, and W. H. Bossert. 1967. Multiple character analysis of *Canis lupus*, *latrans*, and *familiaris*, with a discussion of the relationships of *Canis niger*. *Amer. Zool.* 7:223-232.
- Linnaeus, C. 1758. *Systema Naturae*. . . L. Salvii, Uppsala, ed. 10, vol. 1, 823 pp.
- Makridin, V. P. 1959. Material' po biologii volka v tundrah nenetskogo natsional'nogo okruga. *Zool. Zhur.* 39:1719-1728 (cited from Pulliainen, 1965).
- 1962. [The wolf in the Yamal north]. *Zool. Zhur.* 41: 1413-1417 (translation by Peter Lent).
- Matschie, P. 1908. Chinesische Säugetiere. In *Expedition Filchner nach China und Tibet. Zool-Bot. Ergebn.*, pp. 134-242, pls. vi-xxiv. Berlin.
- Mech, L. D. 1966. The wolves of Isle Royale. *U. S. Nat. Park Serv. Fauna Ser.* 7:1-210.
- 1970. The wolf. *Nat. Hist. Press (Doubleday)*, New York. 389 pp.
- 1973. Wolf numbers in the Superior National Forest of Minnesota. *USDA Forest Serv. Res. Paper, NC-97:1-10* (North Central Forest Exp. Sta., St. Paul, Minnesota).
- Mech, L. D. and Frenzel, L. D., Jr. (ed.). 1971. Ecological studies of the timber wolf in northeastern Minnesota. *USDA Forest Serv. Res. Pap. NC-52:1-62*. North Central Forest Exp. Sta., St. Paul, Minnesota).
- Miller, G. S., Jr. 1912. The names of the large wolves of northern and western North America. *Smithsonian Misc. Coll.* 59(15):1-5.
- Murie, A. 1944. The wolves of Mount McKinley. *U. S. Nat. Park Serv., Fauna Ser.* 5:1-238.
- Nelson, E. W., and E. A. Goldman. 1929. A new wolf from Mexico. *Jour. Mammal.* 10:165-166.
- Ngak, T. 1911. Füchse und Wölfe des Altai. *Zool. Anz.* 35:457-475.
- Novikov, G. A. 1956. Carnivorous mammals of the fauna of the U.S.S.R. *Zool. Inst. Acad. Sci. U.S.S.R.*, Moscow, 284 pp. (The Israel Program for Scientific Translations, Jerusalem, 1962.)
- Nowak, R. M. 1970. Report on the red wolf. *Defenders Wildlife News*, pp. 82-94.
- Oshanin, S. 1971. What will happen to the wolf? *Soviet Life*, pp. 52-55.
- Paradiso, J. L. 1968. Notes on recently collected specimens of east Texas canids, with comments on the speciation and taxonomy of the red wolf. *Amer. Midland Nat.* 80: 529-34.
- Pimlott, D. H. 1967. Wolf predation and ungulate populations. *Amer. Zool.* 7:267-278.
- Pimlott, D. H., J. A. Shannon, and G. B. Kolenosky. 1969. The ecology of the timber wolf in Algonquin Park. *Ontario Dept. Lands Forests Res. Rept. (Wildlife)* 87:1-92.
- Pocock, R. I. 1934. Preliminary diagnoses of some new races of South Arabian Mammals. *Ann. Mag. Nat. Hist. ser.* 10, 14:636.
- 1935. The races of *Canis lupus*. *Proc. Zool. Soc. London*, pp. 647-686.
- Pulliainen, E. 1965. Studies on the wolf (*Canis lupus* L.) in Finland. *Ann. Zool. Fenn.* 2:215-259.
- Rabb, G. B., J. H. Woolpy, and B. E. Ginsburg. 1967. Social relationships in a group of captive wolves. *Amer. Zool.* 7:305-311.
- Rausch, R. A. 1967. Some aspects of the population ecology of wolves, Alaska. *Amer. Zool.* 7:253-265.
- Richardson, J. 1829. *Fauna Boreali Americana*, Josiah Fletcher, Norwich (England), part 1, 300 pp.
- Rutter, R. J., and D. H. Pimlott. 1968. The world of the wolf. J. B. Lippincott Co., Philadelphia and New York, 202 pp.
- Say, T. 1823. Account of an expedition . . . under the command of Maj. S. H. Long (E. James, compiler). Longman, Hurst, Rees, Orme, and Brown, London, vol. 1, 503 pp., vol. 2, 442 pp.
- Schenkel, R. 1947. Expression studies of wolves. *Behaviour* 1:81-129 (unpublished translation from German by Agnes Klassen).
- 1967. Submission: its features and function in the wolf and dog. *Amer. Zool.* 7:319-329.
- Schonberger, D. 1965. Observations on the reproductive biology of the wolf. *Z. Säugetierk.* 30(3):171-178 (translated from German by S. Van Zyll de Jong).
- Schreber, J. C. D. von. 1775. *Die Säugethiere* . . . Erlangen, pl. 89.
- Sclater, P. L. 1874. On the black wolf of Thibet. *Proc. Zool. Soc. London*, pp. 654-655.
- Seal, U. S., and A. W. Erickson. 1969. Phencyclidine hydrochloride immobilization of the Carnivora and other mammals. *Fed. Proc. (Symp. Lab. Anim. Anesthes)* 28:1410-1419.
- Sykes, W. H. 1831. Catalogue of the *Mammalia* of Dukhun (Deccan); with observations on their habits, etc., and characters of new species. *Proc. Zool. Soc. London*, pp. 99-105.
- Tembrock, G. 1963. Acoustic behavior of mammals. Pp. 751-783, in *Acoustic behavior of animals* (R. Busnel, ed.). El Sevier Publishing Co. London, 933 pp.
- Temminck, C. J. 1839. Over de Kennis en de Verbreiding der Zoogdieren van Japan. *Tijdschr. Natuurl. Geschied. Physiol.* 5:284.
- Theberge, J. B., and J. B. Falls. 1967. Howling as a means of communication in timber wolves. *Amer. Zool.* 7:331-338.
- Wagner, A. J. 1841. Die Raubthiere. Supplementband, Abtheilung 2:1-558 (in Schreber, *Die Säugethiere in Abbildungen nach der Natur*).
- Wied-Neuwied, Maximilian. 1841. Reise das Innere Nord-Amerika in den Jahren 1832 bis 1834. J. Hoelscher, Coblenz, 2 vols., 687 pp + map.
- Young, S. 1944. The wolves of North America. *The Amer. Wildlife Inst., Washington, D. C.*, part 1, 386 pp.

The principal editor of this account was S. ANDERSON.

L. D. MECH, MINNESOTA FIELD STATION, PATUXENT WILDLIFE RESEARCH CENTER, U.S. BUREAU OF SPORT FISHERIES AND WILDLIFE (MAILING ADDRESS: NORTH CENTRAL FOREST EXPERIMENT STATION, FARWELL AVE., ST. PAUL, MINNESOTA 55101).